A Dendrochronological Analysis of Insect Outbreaks and Climate Effects on Tamarack from Indiana and Michigan

A thesis

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ABSTRACT

Disturbances have a strong impact on tree stand dynamics across the world. In North America, the larch sawfly (*Pristiphora erichsonii*) and larch casebearer (*Cleophora laricella*) are two non-native species of insects affecting tamarack across much of their native range. The majority of research on the effects of larch sawfly on tamarack (*Larix laricina*) has been conducted in Canada with very little dendrochronological work in the United States along the geographical boundary of tamarack or on the effects of larch casebearer on radial growth. As a consequence, very little is known about the relationship between tamarack and these insects' outbreaks in the United States. The traditional model of Ecological Amplitude in biogeography explains that species are limited along their southern border by species interaction, so it is very important to start to understand the relationship between predator and prey. At the Pigeon River State Fish and Wildlife Area in northern Indiana, tamarack are stressed and dying out on the landscape and local naturalists believe insect outbreaks are a potential factor.

I use the traditional dendrochronological methods to develop and compare host and non-host chronologies from northern Indiana and central Michigan. I then compared these chronologies to each other, local climate variables, and insect outbreak information to better understand climate and outbreak signals in radial growth. I found that tamarack in Indiana showed a stronger negative response to temperature in Indiana than in Michigan which indicates warmer temperature play a role in limiting the southern margin of the species' range. Tamarack also provided a good record of local insect outbreak events. Using outbreak information

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collected from local naturalists, I developed a tree ring outbreak signature for larch casebearer. Continued work along the southern boundary of the species will determine the combined impacts of multiple species specific predators as climate changes.

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PREFACE

The main goal of this paper is to convey the results of my thesis research. This paper starts with an introduction of the hypotheses and research goals of the study. This is followed by a background of tamarack, the history of insect outbreak studies, and the history of studies of tamarack predators in North America to show this study in context of the greater body of research on the topic. The methods and results are then discussed in depth. Finally, the results are interpreted in the discussion and conclusion.

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CHAPTER 1

INTRODUCTION

Fire, wind, insects, and human impact can play vital roles in stand dynamics. By eliminating older, canopy dominant species, disturbances provide openings for new generations of shade intolerant species to take hold. The introduction of exotic species can also fundamentally alter the ecology of an organism. In the last century, tamarack (*Larix laricina*) in North America have been affected by the introduction of exotic defoliating insects. The larch sawfly (*Pristiphora erichsonii*) and larch casebearer (*Cleophora laricella*) have been spreading west across North America since the late 1800's, leaving potentially altered forest resources in their wake (Lejune 1947, Ryan *et al*. 1987). The majority of research on the effects of insect outbreaks on tamarack has been conducted in Canada with very little dendrochronological work examining the southern geographic boundary of tamarack in the United States (Figure 1). There were a few study locations within the United States, however the studies focused primarily on the lifecycle of the insects themselves. Larch casebearer research is also very slim across North America with the majority of studies analyzing the lifecycles of the sawflies and the effectiveness of introduced biological controls for the species.

The traditional model of Ecological Amplitude in biogeography explains that tree species have fairly well established range limited by a certain set of variables (Speer 2010). The northern range limit of tamarack is controlled by temperature (Mamet and Kershaw, 2011), while

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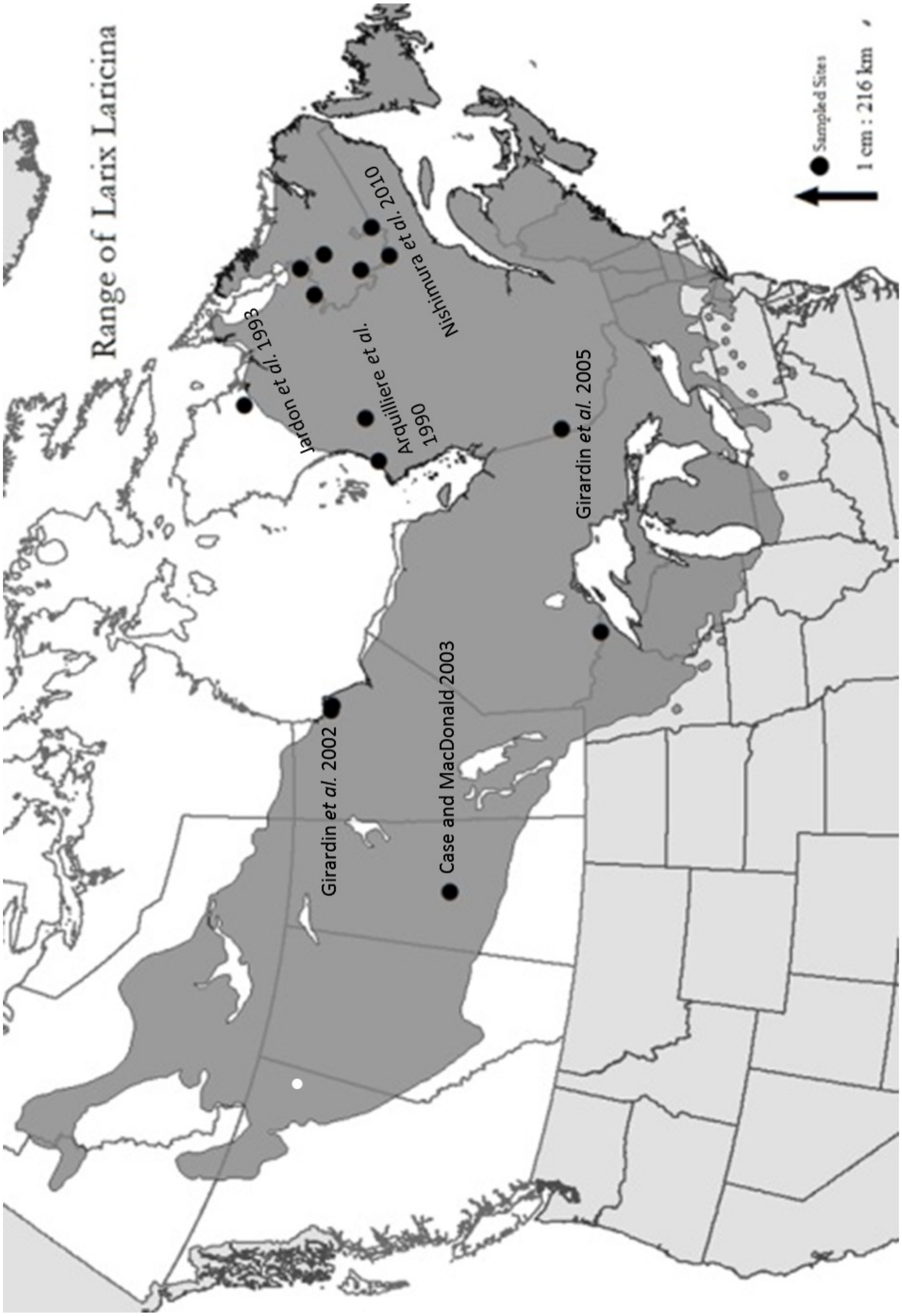

Figure 1. Map of previous studies on tamarack and larch sawfly outbreak studies across North America.

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the southern limit controls are uncertain. At the Pigeon River State Fish and Wildlife Area in northern Indiana, tamarack are dying out on the landscape and local naturalists believe insect outbreaks are a potential driving factor (Richard Dunbar personal correspondence, 2012).

Hypotheses

In order to fully understand the greater ecology and population dynamics of tamarack in North America, we must first understand the control of the species' southern range. Because trees can persist through rapid changes in climate, trees at the southern margin of the species range might provide an opportunity to test hypotheses about how changing climate is affecting tamarack in this southern region. I propose four major hypothesis that are most salient for species management and preservation in Indiana and Michigan.

1) If insect outbreaks are enhanced by warmer temperatures, sites in Indiana will see more frequent or more severe outbreak events than sites in Michigan.
2) If phytophagous insect predation limits tamarack growth along this southern geographic boundary, then a more southerly site would be more affected by insect damage than a more centrally located site.
3) If stand replacement is limited by higher temperatures, there will be fewer saplings in Indiana sites than in Michigan.
4) If tamarack growth along the southern geographic boundary is limited by temperature, tamarack will become more sensitive over time as climate change causes increased annual temperatures in this region.

This study worked towards the following objectives: 1) Examine the current position of the southern climate boundary for tamarack, 2) Examine the effects of climate on tamarack growth, 3) Assess stand replacement in northern Indiana and central Michigan, 4) Determine the

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outbreak signature of larch casebearer for the first time in tree ring series, 5) Identify and determine the severity of larch sawfly and casebearer outbreaks in each location, and 6) Explore driving climatic controls for larch sawfly and casebearer outbreak events.

Chapter 2

BACKGROUND

Tamarack

Tamarack is a shade intolerant deciduous conifer capable of growing in a broad range of environments. It can be found in areas where the coldest temperature is between -33°C and -3°C, highest temperatures between 8°C and 22°C, and annual precipitation between 18 and 140 cm per year (Figure 2) (Johnston 1990). It is outcompeted on more favorable sites by more shade tolerant species and is generally found on marginal mossy hummocks in bogs (Nairn *et al.* 1962, Johnston 1990, Heinselman 1994). Stands tend to be fairly open but can form dense structures when light is readily available after a disturbance (Graham 1956, Nairn *et al.* 1962). Tamarack is commonly found in tamarack dominated and tamarack-spruce (*Picea spps.*) forests, and is less commonly found in black ash (*Fraxinus nigra*)- American elm (*Ulmus Americana*)- red maple (*Acer rubrum*) forest type. The range of tamarack reaches from Connecticut and Indiana at the southern extent, to their northern extent at tree line along Hudson Bay and in Central Alaska (Figure 2) (Johnston 1990). This figure shows where and in what climates tamarack can be found in North America. By superimposing a species range map over climate data at one degree intervals north and south, Thompson *et al.* examined what climate conditions are most favorable to tamarack growth (1999).

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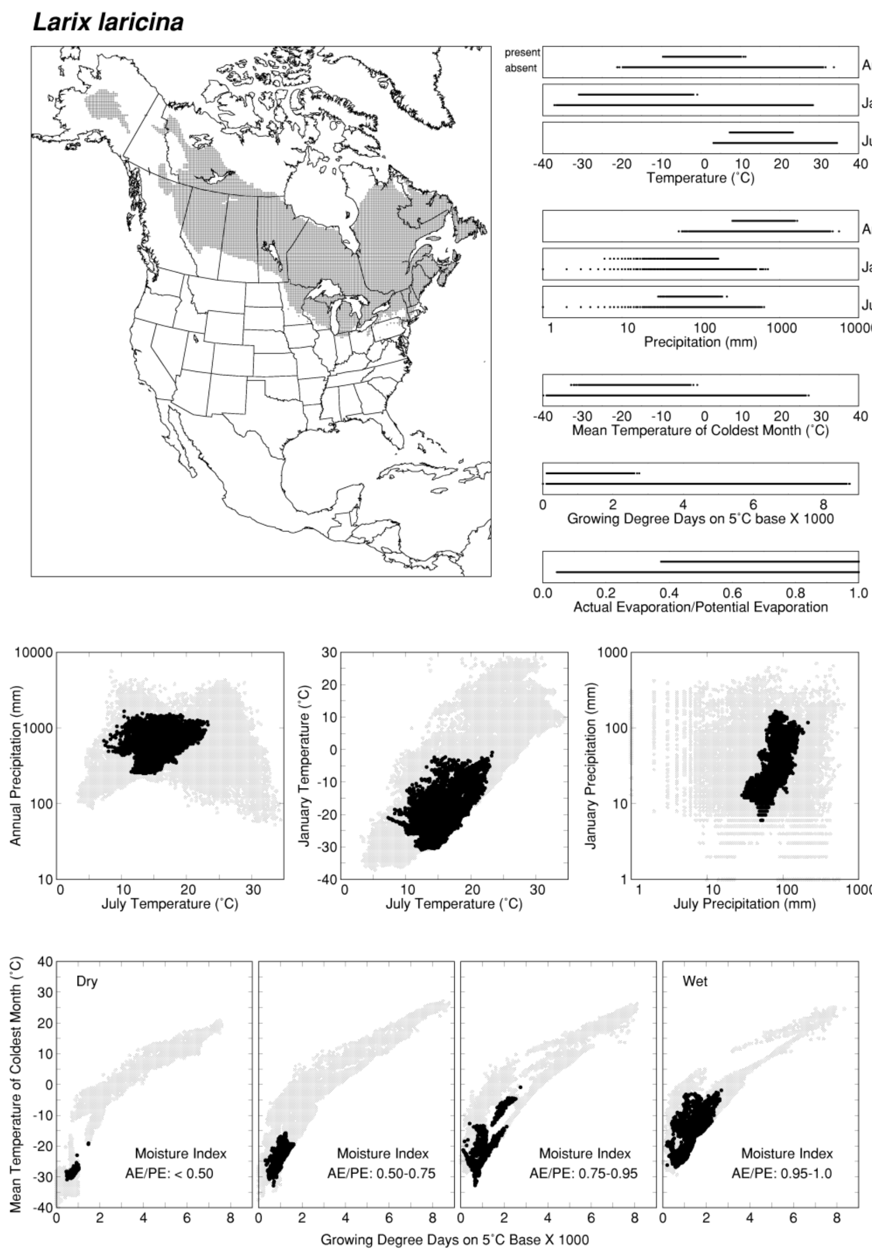

Figure 2. a) A range map showing the distribution of points where tamarack are present, b) Plots showing the climate where tamarack are present (top line) and absent (bottom line), and c) bivariate plots illustrating potential interactions between tree and climate with points where tamarack are present in black and absent in grey (Thompson *et al.* 1999).

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Tamarack is a fairly prolific species. The species is one of the first to flower in the spring producing flower cones in mid to late April in eastern Canada (Johnston 1990). They usually organic rich soil, and a light cover of grass (Johnston 1990). If seeds are germinated under produce cone crops every three to six years. Many cones can contain as many as 40 seeds, but usually one to eight of those are viable due to problems with pollination, frost, predation, or or other factors (Johnston 1990). Seeds can remain viable for four years when stored at optimal temperature and moisture levels (Johnston 1990). Seeds germinate best in warm, moist mineral shade or in fully stocked conditions, they may grow between one and three centimeters but will not survive past six years of continuous shade (Johnston 1990).

Tamarack is an early pioneer species which commonly colonizes former farm fields in Ontario, recently burned bogs, and swampy organic environments across Michigan and northern Indiana (Johnson 1990). As the species begins colonizing an area, the stand structure maintains an open canopy structure, but as the stand matures, it can become fairly dense. Mature stands of tamarack will eventually be outcompeted by shade tolerant conifer or hardwood species such as spruce, cedar (*Thuja spps.*), black ash, American elm, or red maple (Graham 1956, Johnston 1990, Kost 2001). Tamarack growing in Indiana are located at the southern extent of the species' geographic range and are commonly found with black ash, American elm, and red maple.

Insect Outbreaks

Previous studies have examined the effects of a wide array of phytophagous species including, but not limited to, spruce budworm (*Choristoneura fumiferana*) (Swetnam *et al.* 1985), tussock moth (*Hemerocampa pseudotsugata*) (Swetnam *et al.* 1985), Pandora moth (*Colorada pandora*) (Speer 2001), forest tent caterpillar (*Malacosoma disstra*) (Sutton *et al.*

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2007), and those examined in this study. Phytophagous insects can affect evergreens and deciduous trees alike with varying severity for each species of insect and species of tree. The spruce budworm for example is fairly devastating to populations of balsam fir (*Abies balsamea*) causing considerable defoliation leading to mortality rates of nearly 100% (Blais 1954, 1962), while spruce populations were affected less severely (Blais 1983). Because defoliators are reducing the tree's photosynthetic ability, radial growth is reduced for this outbreak period (Frits 1974). In many instances these outbreaks can cause the complete loss of a ring in the tree for a given year (Girardin *et al.* 2002, Girardin *et al.* 2005). This can lead to death in individual trees if the outbreak severity persists, but often times trees will survive the outbreak (Blais 1962).

The trees that survive the outbreak event will retain a growth signature which can lead to future identification of the outbreak event in that host tree (Swetnam *et al.* 1985). When these suppressions in radial growth are observed, it is important to verify that insect caused defoliation is the cause of the suppression and not some other climactic or environmental factor. By comparing the series to a non-host chronology collected within the site, additional factors on growth can be accounted for (Swetnam *et al.* 1985). The non-host chronology will provide an expected growth rate for host species in the site. For instance, if an outbreak were to occur during a drought event, host and non-host species would show suppressed growth caused by the drought. However when ring-widths of the host are compared to those of the non-host and the reduction in growth is more severe, indicating an additional suppressing factor on the growth of the host species (Swetnam *et al.* 1985).

The duration and intensity of outbreak events vary between insects and consequently, they produce different signatures in the ring-widths. For example, the spruce budworm produces a very identifiable pattern which consists of a suppression lasting between five and 20 years and

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a reduction of growth of at least -1.28 standard deviations from the mean (Swetnam *et al.* 1985, Swetnam and Lynch 1993, Boulanger and Arseneault 2004). Additional indicators include traumatic resin ducts or a lightening of the latewood portion of the ring (Jardon *et al.* 1994, Schweingruber *et al.* 2008). Studies by Girardin *et al.* (2005) and Huang *et al.* (2010) have shown pale late-woods are frequently associated with outbreaks of phytophagous insects in tamarack, spruce, aspen (*Populus tremuloides*), and a variety of other species. The mechanism for the development of light rings has not been explored in depth, but with the exception of one study by Arquilliere *et al.* (1990), many studies have identified pale late-woods in periods of historic and reconstructed outbreak events (Jardon *et al.* 1994, Girardin *et al.* 2001, Case and MacDonald 2003, Girardin *et al.* 2005, Huang *et al.* 2010). The presence of light rings also follow a latitudinal gradient where they are more common in southern regions than regions farther north (Huang *et al.* 2010).

By using these techniques to identify historical outbreak events, scientists can examine the spatial extent, periodicity, and synchronicity of outbreak events. Studies in spruce budworm have determined that spruce budworm outbreaks have a return interval of around 40 years and have a fairly broad distribution during major outbreak events (Figure 3) (Boulanger and Arseneault 2004, Bouchard and Pothier 2010). I explored similar patterns in larch sawfly outbreaks reported in the record, however few synchronous outbreak events were observed.

Insect outbreaks of defoliating insects have also been studied in Europe. Esper *et al.* (2007) studied the effects of larch budmoth (*Zeiraphera diniana*) on European larch (*Larix decidua*). Using living and archeological samples, they were able to reconstruct 123 larch budmoth outbreaks using variations in the density of latewood rings. They determined that

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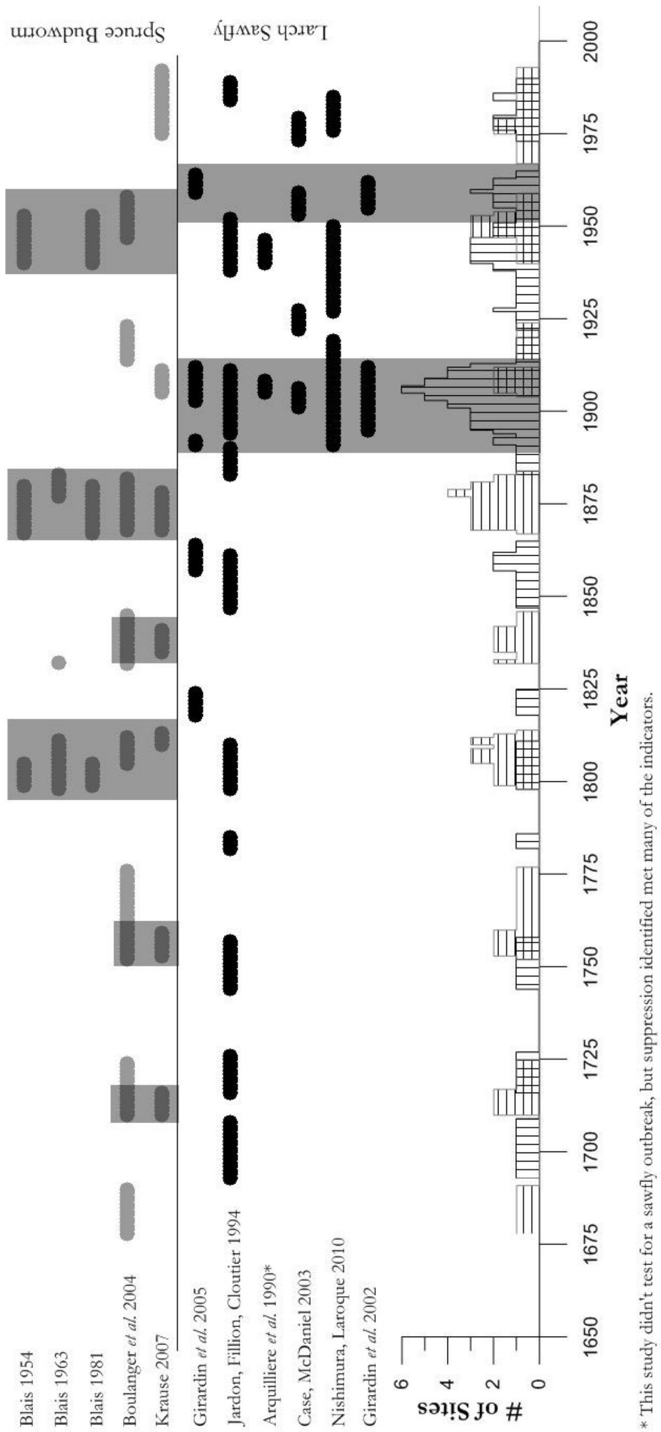

Figure 3: Graphs showing the outbreak events of spruce budworm and larch sawfly. The graph on the bottom of the figure shows the number of locations recording an outbreak in horizontal lines and vertical lines for spruce budworm and larch sawfly outbreaks respectively. The darker grey boxes indicate periods of more synchronous outbreak events.

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latewood density decreased during outbreak events and major outbreaks occurred every 8-9 years.

The Larch Sawfly

The larch sawfly can be found across much of the range of larch in Japan, Russia, Great Britain, and North America (Coppel and Leius 1955). In the native range of larch in alpine Europe, the species is well controlled by myriad of natural parasites (Tunnock 1972). It is an herbivorous insect responsible for 60% to 100% defoliation during outbreak events (Coppel and Leius 1955, Graham 1956). The insect has a two-year life cycle. Adult sawflies deposit their eggs in a groove using an ovipositor on the new terminal shoots of the larch (Lejune 1955, Graham 1956). This groove will cause the branches to grow in a twisted fashion, creating visual evidence of a recent sawfly outbreak event (Graham 1956). The eggs hatch soon after being laid and the greenish larvae consume needles in an outward pattern from the terminal shoot until the larvae are fully grown (Lejune 1955 and Graham 1956). In late July and August, the fully grown larvae drop from the tree and burrow into the mossy duff beneath the tree (Lejune 1955 and Graham 1956). The insects spend the winter at a depth where moisture is enough to prevent desiccation while in diapause through the winter months, but at a depth where spring moisture will not drown the pupa (Lejune 1955). As temperatures warm, the pupa will metamorphose into the adult fly stage and continue the cycle. Most of individuals will emerge from the diapause state as full grown adult flies, with only 5-6% remaining in diapause until the following season (Graham 1956). Population levels fluctuate fairly frequently but outbreak population densities can be reached in as little as three years from the beginning of population growth (Tailleux and Cloutier 1992).

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As the pupae develop, their resistance to immersion increases from dying within a week underwater in the fall, to surviving multiple weeks of submersion in the spring (Lejune 1955). This resistance provides a line of defense in the spring snow melt but leaves the insect vulnerable to late growth season high precipitation events. Though the cocoon can protect the pupa for some time, the insect is still vulnerable to parasitism from a variety of pests and consumption by small mammals (Turnock 1972). To attempt to control the spread and severity of the larch sawfly, managers in Canada released *Mesoleius tenthredinis*, a strain of parasite that attacks the larvae, in Manitoba, Ontario, and Saskatchewan. It was also released in Nova Scotia and New Brunswick in the 1930's and spread rapidly as well (Turnock 1972). The larch sawfly was discovered in the cordilleran region of North America in 1930 and *M. Tenthredinis* was released shortly thereafter in British Columbia in 1934. This parasite was quite effective until a resistant strain of sawfly became dominant after about 30 years and the effectiveness diminished (Turnock 1972). *M. tenthredinis* is still quite effective in cordilleran regions of North America, and other species of parasites still play a role in controlling sawfly populations at lower elevations.

There have been quite a few studies on the spatial distribution and severity of larch sawfly outbreaks. Long term records collected by Jardon *et al.* (1994) and Girardin *et al.* (2002) indicate larch sawfly outbreaks have occurred in North America as early as the beginning of the 18th and 19th centuries. The earliest suppressions were not confirmed due to the lack of non-host data to account for changes in climate. The earliest well replicated outbreak was from 1744 to 1749 (Arquilliere *et al.* 1990, Jardon *et al.* 1994, Girardin *et al.* 2002, Case and McDaniel 2003, Girardin *et al.* 2005, Nishimura and Laroque 2010). These records are distributed across the

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central and northern ranges of tamarack's geographic distribution. One area where the records did not cover was the southern regions of the species.

Many young tamarack are able to survive larch sawfly outbreaks, however, mature trees are less likely to withstand severe outbreaks. Mature tamaracks can have mortality rates ranging from 60% to 100% when they are greater than 12.5 cm diameter at breast height (DBH) (Graham 1956). Young trees are generally vital enough to produce new shoots and needle year after year during an outbreak, while mature trees are significantly more dependent on the existing infrastructure of the tree (Turnock 1972). This sensitivity of mature individuals makes reconstructing severe outbreaks at long time scales quite difficult. However, less devastating outbreaks farther north produce fewer mortalities in mature trees and affect young trees very little. The trees that survive the outbreak events are generally unable to produce enough nutrients to grow a normal sized ring, or any ring at all (Jardon *et al* 1994). The ability to survive multiple outbreaks allows trees to record multiple outbreak events through very distinct ring width patterns indicative of an outbreak event (Nairn *et al.* 1962). Outbreaks begin to be recorded in radial growth one to two years after the initiation of the outbreak (Tailleux and Cloutier 1992).

Larch sawfly outbreaks can be identified in tree rings by a number of indicators: 1) a light latewood band in the first year of an outbreak, 2) a suppression of growth of over 1.28 standard deviations from the mean, and 3) missing rings during a suppression lasting between 4 and 16 years (Jardon *et al.* 1994). It is important to verify the growth signatures with modern outbreak information because not every outbreak has all of these indicators and climatically derived suppressions may resemble insect outbreak signatures. A comparison between the host and non-host species with similar climate response will also check for suppressions caused by climate.

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This method of identifying larch sawfly outbreaks has been successful in identifying potential outbreaks from 1744 to the 1970's across much of the species range (Jardon *et al.* 1994, Girardin *et al.* 2002, Case and MacDonald 2003, Nishimura and Laroque 2010). The characteristics of the earliest larch sawfly events have led to a theory that there are some native populations of larch sawfly. However, due to a lack of replication of these early events, and little comparison with non-host species, the description of these events remain under supported. Many studies show an outbreak event starting between 1891 and 1901 and lasting between 4 and 29 years, followed by various asynchronous events centered around the 1950's, 1970's, and current times (Arquilliere *et al.* 1990, Jardon *et al.* 1994, Girardin *et al.* 2001, Girardin *et al.* 2002, Case and McDaniel 2003, Girardin *et al.* 2005, Nishimura and Laroque 2010). Larch sawfly can also have a strong effect on regeneration in tamarack by clearing mature trees to allow for open spaces in which new growth can initiate (Nairn *et al.* 1966, Girardin *et al.* 2002, Case and MacDonald 2003). This pattern follows many of the traditional disturbance patterns where growth is limited competition for sunlight.

The Larch Casebearer

The larch casebearer (*Cleophora laricella*) is another introduced defoliator of tamarack in North America. The larch casebearer is native to the Alps region of Europe. Here, populations are controlled by an assortment of native parasites and pathogens (Ryan *et al.*1987). It was first identified in the United States in 1886 in Massachusetts. By the 1920's and 1930's the casebearer had started to affect tamarack in the lake states. In 1957 the larch casebearer was identified affecting mountain larch (*Larix occidentalis*) in the Rocky Mountains of Idaho and by the 1970's, mountain larch were being affected across nearly their entire range (Ryan *et al.* 1987; Alfaro *et al.* 1991).

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The larch casebearer has a two year life cycle consisting of four larval instar (physical shape), and one adult stage. In early June, females lay their eggs on a needle, which hatch shortly thereafter. The larvae mine the needles by consuming the contents of the needles. While in the needle, they molt into their second instar and sever the hollow section and use it as a protective husk. The larvae continue to forage on surrounding foliage until late September or October when they molt into their third instar and attach to a woody stem to spend the winter. In the spring, synchronous with the emergence of new tamarack foliage, the fourth instar emerges and continues to forage on vegetation and eventually molts to the adult stage to lay eggs and initiate the next generation of casebearer (Alfaro *et al.* 1991). The spring defoliation can be more severe as the larger larvae forage more intensely than the smaller, newly emerged larvae (Alfaro *et al.* 1991).

Mortality caused directly by the larch casebearer is rarely seen. The defoliation during an outbreak event can reduce radial growth by 50% to 97% after five consecutive years of outbreak conditions (Ryan *et al.* 1987). If outbreaks are allowed to continue severely for a sustained period of time, mortality can be observed in branch tips, branches, tree tops, or entire trees with increasing duration of outbreak respectively (Ryan *et al.* 1987). Despite the severe impact to radial growth, mature trees are less likely to die from the outbreak, but more likely to die from simultaneous effects from another form of disturbance like drought, other insects, or infections. Mortality is more likely seen in open-grown, younger trees (Ryan *et al.* 1987). A study performed by Benoit and Blais (1988) found a response to defoliation in the annual radial growth, but no studies have developed a tree-ring signature caused by larch casebearer outbreaks.

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Eastern Larch Beetle

The eastern larch beetle is an insect native to North America and has historically been fairly innocuous until the middle of the last century. Mortality began to be reported in the early seventies as the beetle started to kill large tracks of tamarack (Seybold *et al.* 2002). Outbreaks were killing upward of 50% of the tamarack in the stands.

The eastern larch beetle overwinter in the bark of the infected tree (Seybold *et al.* 2002). The adults move to a new host tree and burrow into the phloem. While in the phloem they burrow up and down and carve out lateral egg galleries in which the females will deposit their eggs. The larvae will grow and develop into their adult stages, emerge from the tree, and move to new host trees. Each generation takes between 60 and 70 days from eggs to adult so multiple generations can occur each year (Seybold *et al.* 2002). The outbreaks can start with beetle populations in cut and downed wood and transfer to living stands as the population level grows (Langor and Raske 1989). A portion of the infected trees (~50%) will prematurely turn yellow in August or September (Langor and Raske 1989). Published and unpublished studies cited by Langor and Raske (1989) would conduct aerial and land based surveys looking for these early yellowing trees to define outbreak intensity and distribution. Outbreaks of eastern larch beetles are frequently preceded by a defoliation event, either from insects such as the larch sawfly or larch casebearer, between one and three years before the initiation of the beetle outbreak (Turnock 1972, Seybold *et al.* 2002).

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Chapter 3

METHODS

Site Description

Temperatures in northern Indiana range from lows around 17°C to highs around 27°C in the summer months and lows of -6°C and highs of 1°C in the winter months. Precipitation is 939 mm per year with May being the wettest month with 3225 mm of rain in the month. The northern part of Indiana generally receives between 355mm and as much as 1930mm of snow in the snow belt region near Lake Michigan (Indiana State Climate Office). The Northern Unit of Indiana forests, comprising nearly 60% of the state, contains Maple-Beach, Oak-Hickory, and Elm-Ash-Cottonwood, representing 45%, 27%, and 23% of the total forest cover, respectively (Tormoehlen *et al.* 2000). In central Michigan, annual temperatures range from 15°C and 28°C in the hottest month of July, to -9°C and -1°C in the coldest month of January. The average annual precipitation in central Michigan is 785mm with the most of the precipitation in the spring (PRISM Climate Group 2011).

Sampling locations were selected using ArcGIS. Land cover types indicative of common tamarack habitats, including marshy woodland and shrub land, were extracted from the 2006 National Land Cover Dataset (Figure 4) (Fry *et al.* 2011). These locations were then verified for common characteristics indicating the presence of tamarack using aerial photographs to select mature and dense looking stands. Particular attention was given to sites that had deciduous cover

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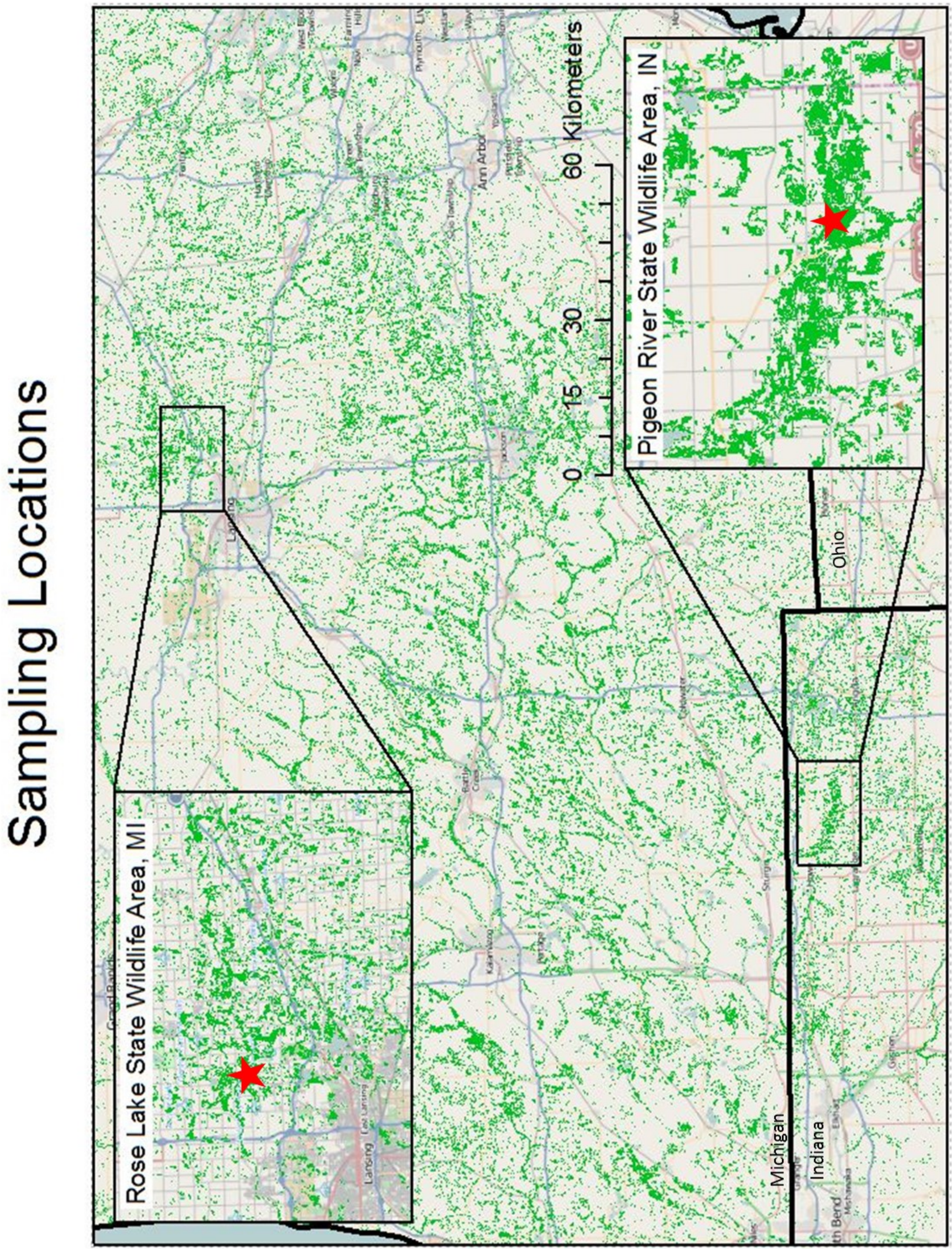

Figure 4. Image of the distribution of environments where tamarack are commonly found (green pixels) and sampling locations (red stars).

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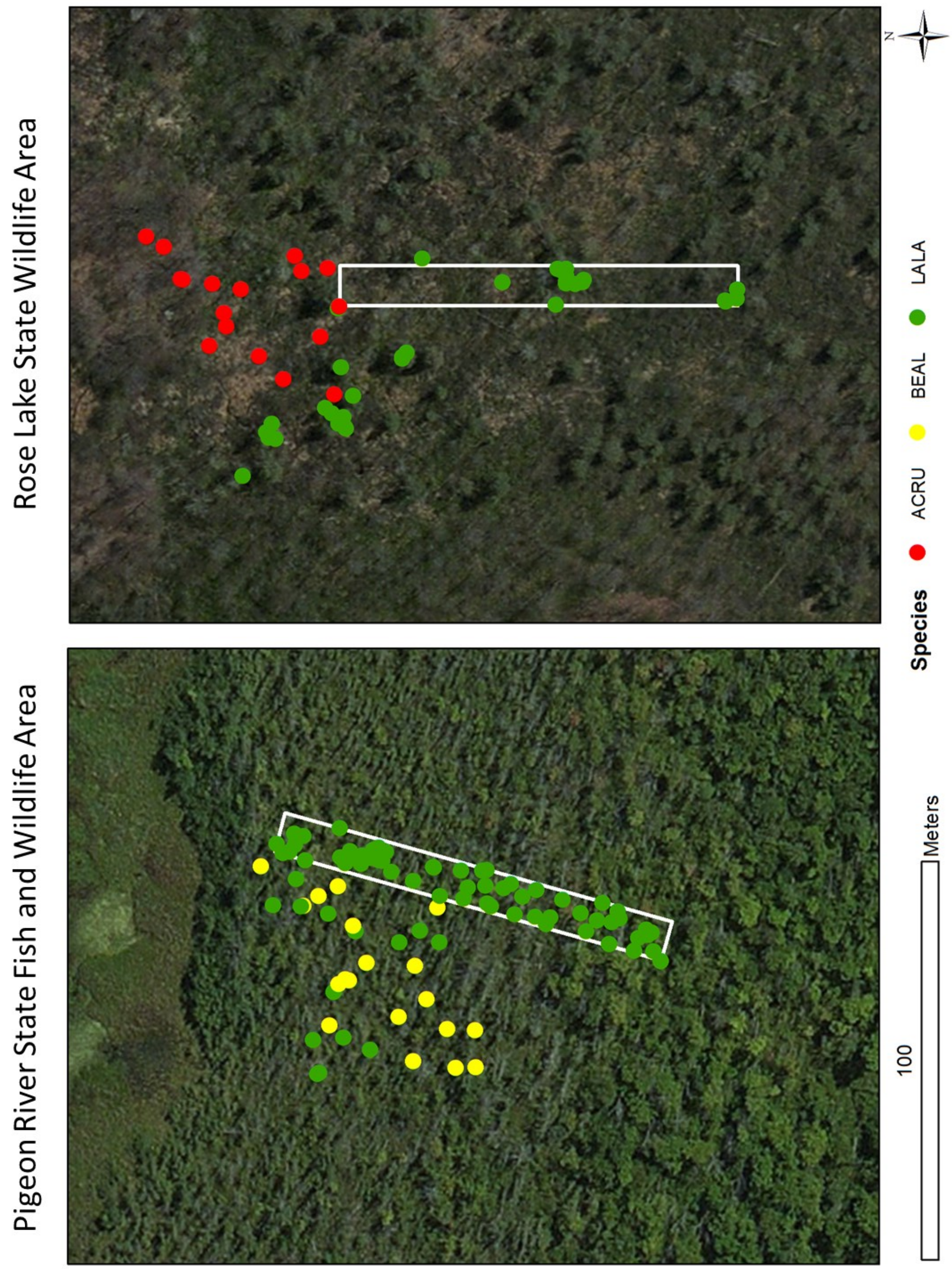

Figure 5. Images of where samples were collected in Indiana (left) and Michigan (right). Species are color coded with green for tamarack, red for red maple, and yellow for yellow birch.

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and whose shadows were long and linear, indicative of coniferous species. To avoid locations with primarily evergreen conifers, images from multiple seasons were used to rule out other conifers because tamarack lose their foliage for winter and spring images. Potential sampling locations were limited to public lands to avoid obtaining permission from many different land owners. The Pigeon River State Wildlife Area in northern Indiana (Figure 4a) and Rose Lake State Wildlife Area (Figure 4b) satisfied the above criterion and were chosen for sampling. The Indiana site is 80km from the southern geographic boundary of tamarack and the Michigan site is 140 km from the geographic range limit. The sites chosen for this study were selected because they lie in the area where rich tamarack swamps are most commonly found (Kost 2001). Talking with the local foresters and land managers in each state was helpful in narrowing down areas that have higher populations of tamarack in each of the locations.

Sample Collection

A regression analysis was conducted between the host, non-host, and three climate variables to determine if the two species have similar growth patterns and similar responses to climate. Yellow birch (*Betula alleghaniensis*) and red maple (*Acer rubrum*) were selected at Pigeon River Fish and Wildlife Area and Rose Lake State Wildlife Area respectively. Samples from host and non-host species were used to develop a chronology free from disturbances caused by larch specific insects to act as a comparative control for climate. Sampling transects were selected by selecting a random starting point in each stand, and creating a 100m transect perpendicular to the hypothesized moisture gradient in each location. Figure 5 shows the location of the transects (white boxes) and the individual tree samples within the transect. The tree locations are color coded for species with red, yellow, and green representing, red maple, yellow birch, and tamarack respectively.

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A variety of sampling techniques were used at each location. In order to obtain information on stand initiation and regeneration, a 100m by 10m band transect was sampled perpendicular to the moisture gradient which theoretically decreases as distances increases from a body of water (Speer 2010). All tamarack were sampled in this transect, including living, dead, and downed trees. In order to develop the longest chronology for insect outbreak reconstruction, targeted sampling was used to obtain cores at breast height from 15 tamarack and 15 non-host trees showing signs of old age (Speer 2010). These trees were identified as having larger trunks, thick upper branches, and potentially scraggy tops (Speer 2010). Cores taken in the band transect for the stand regeneration study were taken at a height of 0.3m to collect the earliest possible date. If rot was present or wood was missing, an additional sample was taken at 1m height or greater to avoid potentially problematic sampling conditions and a lack of data due to rotten or missing wood. Observations were made on the presence of saplings within the band transect, but no saplings were identified. Cross sections from remnant wood were collected with a hand saw and site information was collected (including stand structure, status of individual, and DBH).

Sample Processing

Upon returning to the lab, the samples were air dried, mounted to core mounts and sanded with progressively finer sandpapers, starting with 162 micron (100 grit) and moving to 9 micron sanding film (1800 grit), to ease ring identification by revealing individual cells in the wood (Orvis and Grissino-Mayer 2002). Samples were then dotted for ring count, skeleton plotted to verify ring dates across tree samples (Speer 2010), and measured for total width (TW), earlywood width (EW), and latewood width (LW) at 2800 or 3200 dpi with WinDENDRO (Regent Instruments 2009b). The higher resolution was used for the majority of the samples, but

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a lower resolution setting was required for long samples due to limitations in the image dimensions accepted by the measuring program. In instances where ring boundaries were unclear, a visual comparison with a scope was used to determine the position of the ring boundary. The boundary between early and latewood was defined by the initial onset of latewood formation in order to obtain the timing of senescence. In situations where reaction wood is present, the latewood boundary is placed where the cell walls thicken and first become lignified. Latewood was not measured for the birch or maple chronologies because these species create rings with diffuse pores whose boundaries are marked by parenchyma cells, not thickened, lignified cells.

During the crossdating stage, suppressions in ring width were noted by start and end year of the suppression. These outbreaks were then classified into two classes; larch sawfly and unknown outbreaks. Larch sawfly outbreaks were identified using the aforementioned parameters set forth by Jardon *et al.* (1994). The light latewood definition is a qualitative measure describing the visual appearance of the ring under the microscope used to add a level of biological response to the suppression signal (Girardin *et al.* 2005). The remaining outbreaks classified as unknown were compared to historical records of area and regional insect outbreak and defoliation records obtained from local naturalists and records of percent defoliation. Ring anomalies including light latewood and traumatic resin ducts were also noted to get a better understanding of what effects these outbreaks have on ring morphology. These identification parameters are not guaranteed to occur in all outbreaks so suspected outbreaks were supported using a comparison with a non-host species and historical records (Case and MacDonald 2003, Girardin *et al.* 2005).

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Dating of the tree-ring material was conducted using the skeleton plot and memorization methods of crossdating (Speer 2010). After ring-counting and dotting, individual samples were visually skeleton plotted and compared to develop a working master chronology. Adjustments to dating were made after visual inspection of the characteristic patterns observed in the ring-widths in comparison with other dated samples. After a working master was developed, any additional samples were dated to the working master using the memorization of significant years. Dating was verified using the computer program COFECHA. The program develops a master chronology free from low frequency variation using a 32 year or 50% spline, compares the individual series to the master chronology using a correlation analysis, and outputs a file containing descriptive statistics of the individual and mean chronology (Grissino-Mayer 2001). To aid in dating, an additional section is created for samples below the calculated significance level containing correlation values for a ten year window on either side of the dated segment (±10) showing where the sample might better align (Grissino-Mayer 2001). Any suggested corrections were only taken if visual evidence in the tree-rings supported the change (missing, micro, or false rings). No missing or false rings were blindly inserted.

COFECHA also calculates mean sensitivity of the master chronology. This value represents mean percentage change between annual ring widths for the entire series. Higher sensitivity values indicate higher inter-annual variation in the rings, indicating a stronger response to an environmental condition, whereas lower values indicate complacency to growth factors (Fritts 1976). Low mean sensitivity values range between 0.10 and 0.19 while values above 0.30 are considered high (Grissino-Mayer 2001). Medium to high values can be beneficial, but when values are above 0.4, they can be very difficult to date (Speer 2010). This measure can be used to examine how well trees respond to their surroundings, however these

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suppositions require additional analysis to determine the underlying factors in the inter-annual variation.

(1) Schweingruber 1988

$$\text{Annual } S_{i+1} = \frac{(X_{i+1} - X_i) \cdot 2}{(X_{i+1} + X_i)} \text{ ; mean } S = \frac{\sum_{i=1}^{n-1} [S_i + 1]}{n-1}$$

The samples were standardized in R ver. 3.0 (R Core Team 2008) using the i.detrend() function obtained from the Dendro Program Library in R (dplR) (Bunn 2008) in R (R Development Core Team 2008). The i.detrend() function allows for the selection of one of three standardization methods, a user defined cubic smoothing spline, negative exponential equation, or horizontal line, for each series in the data file. For this study, a 40 year smoothing spline was used to remove growth related trends while maintaining 99% of variation at 12.67 years (Cook *et al.* 1985, Speer 2010). Because the outbreaks generally last between 4 and 16 years, the majority of any variation caused by insect outbreaks was maintained. If this model created negative or extreme indices, a horizontal line model was used to prevent artificial increases or decreases to ring width indices cause by a poor model choice and preserve the natural ring-width patterns seen in the wood. After detrending the data, the chron() function (Bunn 2008) was used to develop a robust mean (standard) and autoregressive residual chronologies. ARSTAN Ver. 6.05 (Cook *et al.* 1985) was used to create chronologies for individual trees by averaging the samples' indices into one set of data per tree. The chronology created can be used in the OUTBREAK (Swetnam *et al.* 1985) because the program analyzes the ring-width data from each individual tree in the site.

Climate analysis was conducted using the R functions dcc() and mdcc() functions in the package bootRes (Zang 2012). Analyses were conducted between precipitation, temperature, and Palmer Drought Severity Indices (PDSI) and earlywood, latewood, and total ring widths.

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The dcc() function calculates the response and correlation functions for the provided tree-ring and climate variables. A set of plots for each of the climate responses was created for each of the ring-width series using the dcplot() function. Moving response and correlation analyses were conducted using a 25-year window in the mdcc() function and plotted using mdcplot(). Plots from these analyses show correlation values for 24 year windows from the beginning of the record to the end. Positive and negative values are depicted in blue and red respectively with decreasing color intensity showing decreasing correlation values. These functions create outputs similar to the software DendroClim (2002). A confidence interval of 95% was used for all statistical analyses.

Insect outbreaks were quantified using the computer program OUTBREAK (Swetnam *et al.* 1985). OUTBREAK compares the host data set to a non-host data set. The parameters for Larch sawfly outbreaks included a suppression of -1.28 standard deviation from normal growth for a duration of 4-15 years (Girardin *et al.* 2005). In the case of the larch casebearer and eastern larch borer, OUTBREAK was used to develop a set of parameters to quantify larch casebearer outbreaks. An α of 0.05 was used for any statistical analysis.

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Chapter 4

RESULTS

Chronologies

The collected samples were used to create two chronologies at two sites, ranging in length from 55 to 112 years. The tamarack chronologies developed in this study covered a large period of time for eastern forests, covering 113 and 90 years in Indiana and Michigan respectively. The non-host chronologies covered 63 and 55 years in the Indiana and Michigan sites respectively (Table 1). The mean series intercorrelation values (MSI) for the tamarack earlywood, latewood, total width, and birch total width chronologies from Tamarack Bog range from 0.482 and 0.558. The MSI for the tamarack chronologies from Rose Lake are comparable, ranging from 0.406 to 0.578, with maple having the highest MSI (Table 1). The chronologies from Tamarack Bog had mean sensitivity (MS) values between 0.367 and 0.445. MS values from Rose Lake were slightly lower ranging from 0.317 to 0.403. Tamarack Bog had a large number of dead trees which were cored in this study and in many cases, the outer 15 to 20 years of the trees were too rotten to retain for dating. Consequently, this creates a peak in the number of samples in the middle of the data series.

Stand Age Structure

Stand structures in both Tamarack Bog and Rose Lake resembled those described in the literature (Kost *et al.* 2010). Tamarack Bog had a semi-open canopy structure with a fair amount

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Table 1. Inter-series correlation, mean sensitivity values and chronology ranges. Tamarack chronologies are marked with a star.

	MSI	Mean Sensitivity	Range
Tamarack Bog			
Earlywood ★	0.548	0.400	1910-2013
Latewood ★	0.482	0.445	1910-2013
Total Width ★	0.558	0.367	1910-2013
Birch Total Width	0.514	0.408	1950-2013
Rose Lake			
Earlywood ★	0.544	0.372	1924-2013
Latewood ★	0.406	0.403	1924-2013
Total Width ★	0.527	0.317	1924-2013
Maple Total Width	0.578	0.382	1959-2013

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of understory reeds and poison sumac (*Toxicodendron vernix*). The dominant tree species on the landscape were tamarack, yellow birch, and rock elm (*Ulmus thomasii*) with a few red maple scattered around the stand. The angiosperms seemed in healthy condition with wide canopies. The majority of tamarack had significant die back of upper and outer limbs with the majority of the living needles located on small branches on the trunk or on larch primary branches (Figure 6).

Rose Lake had a dense canopy dominated by tamarack and red maple with a variety of dense understory species. The angiosperms in the location seemed quite healthy as well, growing vertically with little expansion in the canopy. The tamarack were doing well in this area as well, having healthy outer branches with some self-pruning in areas with higher amounts of shade (Figure 7). Thirty minutes were spent in each of the two locations searching for seedlings to establish one meter sampling locations, but no seedlings or saplings were observed in either site and only five samples have a DBH of less than 2.5cm.

Tamarack populations in the Tamarack Bog transect were fairly mature. There were two distinct cohorts of recruitment in this site: one from 1915 to 1920 and another around 1950 (Figure 8). Recruitment after 1950 was fairly steady until 1980 when there was a halt to recruitment. An increase in radial growth after 2008 can also be observed in the data in both the birch and tamarack chronologies at this site (Figure 8). Though the chronology at Rose Lake is not as old, similar patterns were observed in tamarack from Michigan. Rose Lake experienced a strong recruitment event in the early 1950's and then tree recruitment tapers off to 2000 where no new individuals are establishing on the site (Figure 9). Increases in radial growth in the latter part of the last decade resemble those of tamarack at Tamarack Bog, although they are not to the same amplitude.

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Figure 6. Example of damaged tamarack and open canopy in Tamarack Bog, IN.

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Figure 7. Example of the forest at Rose Lake, MI. Notice the tamarack in the background and the dense foliage of red maple and understory species.

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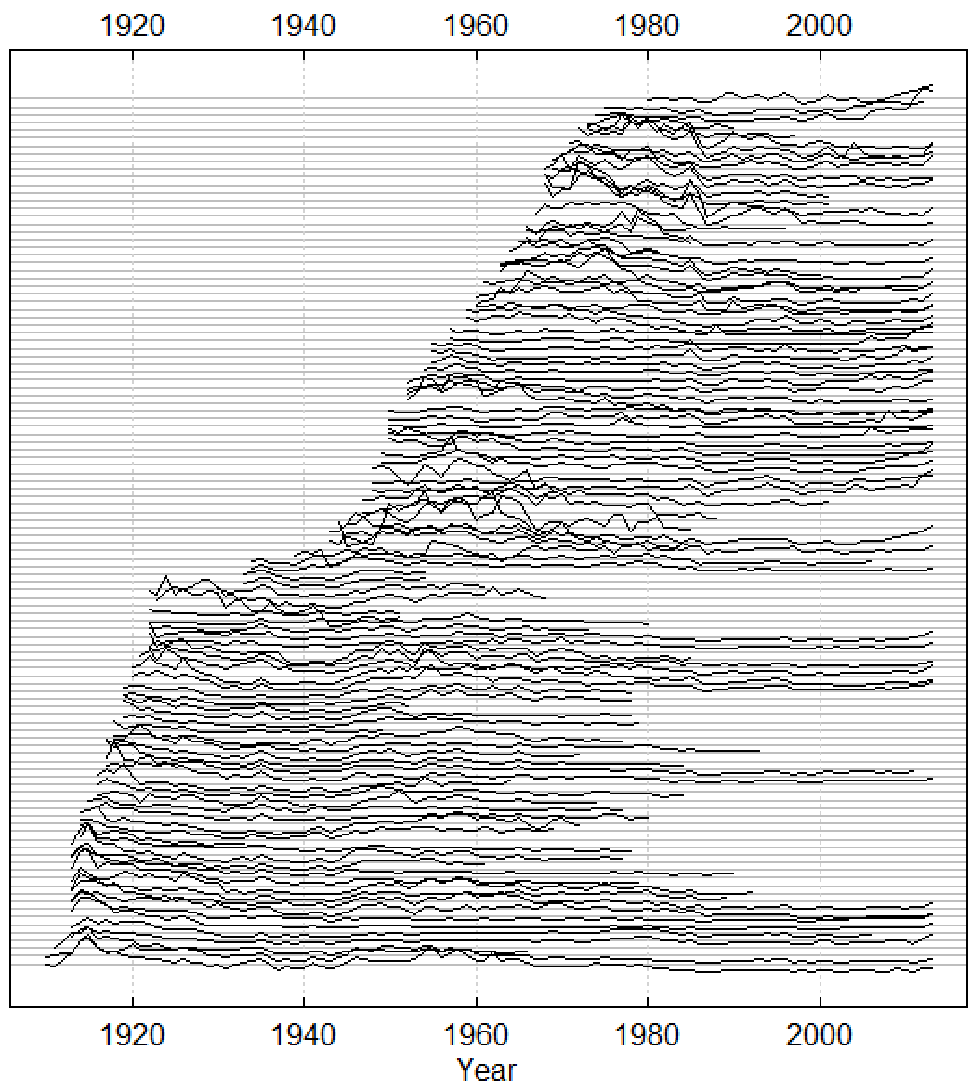

Figure 8. Spaghetti plot of samples at Tamarack Bog showing the beginning and end date of each core with raw ring-width on the y-axis. Note the establishment dates indicated by the beginning date of each core with a distinct establishment pulse from 1915 to 1920.

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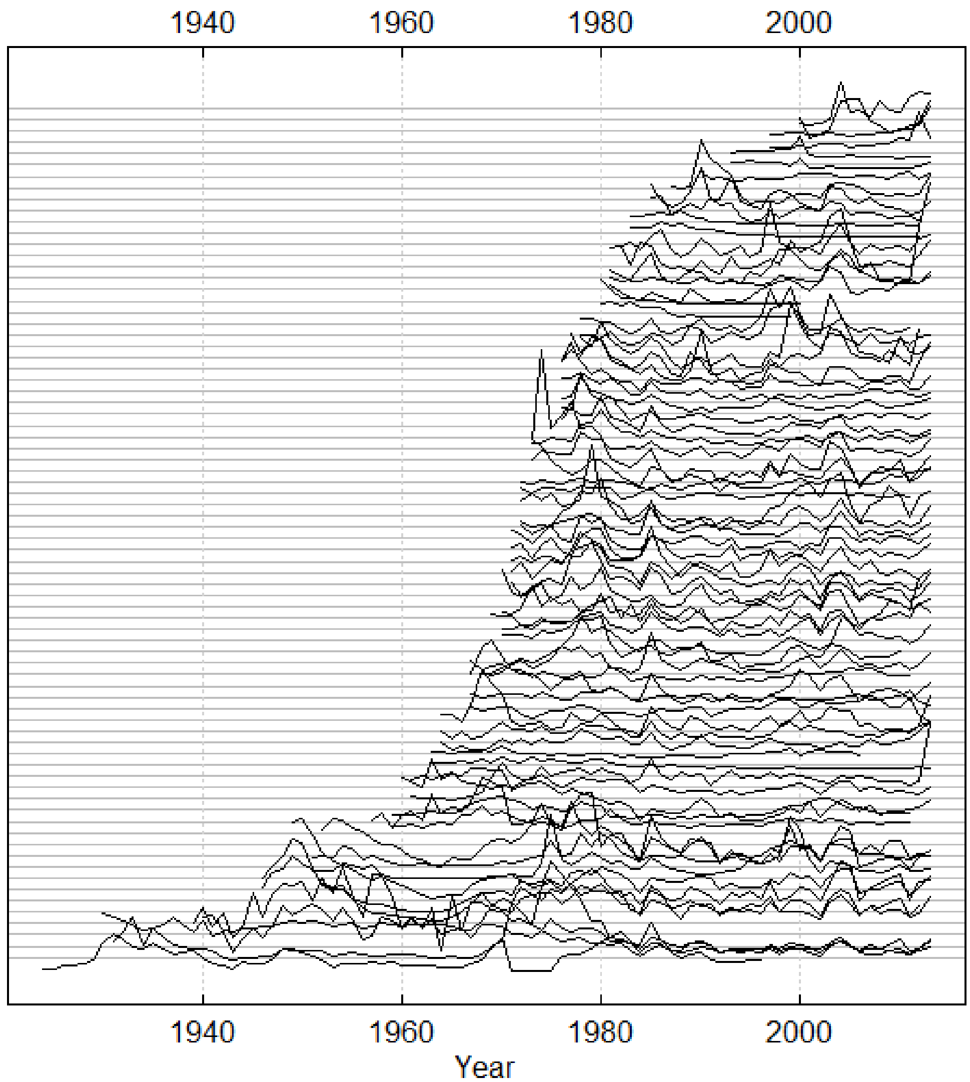

Figure 9. Spaghetti plot of samples at Rose Lake showing the beginning and end of each core with raw ring-width on the y-axis. Note the low number of samples extending before1970 and the establishment pulse from 1960 to 1980.

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Identification of Outbreaks

Three major periods of suppression were identified at Tamarack Bog. The most recent suppressions, 1986-1990, and 1997-2002, were recorded by 53% and 86% of the trees in the transect. The years with the most missing rings are 1986, 1987, 1997, 1998, and 2002. They are missing from 21%, 35%, 17%, 23%, and 16% of the samples respectively. There are other missing rings throughout the samples, however they are missing from fewer than ten percent of the samples. These other missing rings are found in areas of sustained suppression in cores which lack a complete return to expected growth. Though no quantitative records of outbreaks in these areas exist, accounts of defoliation from local naturalists indicate larch casebearer was present at outbreak levels in 1987, 1989, and became less frequent through time (Dunbar, personal correspondence 2014). A study in 1989 observed larch casebearer on all tamarack and yellowing of large trees along the river in June. These large yellowed trees died in subsequent years (Dunbar personal correspondence 2014). Ring-growth in 2012 and 2013 started trending towards average growth.

In addition to growth suppressions, qualitative indicators of defoliation were also observed in the 1986 and 1997 outbreak events. In each suppression, small rings with thin latewood were observed in the first two or three years of the suppressed period (Figure 10). In addition to these rings, other cores had rings which lacked complete lignification of latewood cells (Figure 10A). The two most recent outbreaks were well covered by the non-host chronology. However, the suppression from 1931-1943 was not covered by the non-host chronology. A comparison of growth to moving climate response for this period shows trees are responding negatively to current June temperature (Figure 12). Similar climate responses to June and July temperatures are also present starting in 1985 (Figure 13 and 14).

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Figure 10. Image of a suppression in a standing snag which died in 1997 at Tamarack Bog. A)Traumatic resin ducts at the beginning of the suppression and rings with poorly developed latewood. B) Suppressed period with small rings and poorly lignified latewood.

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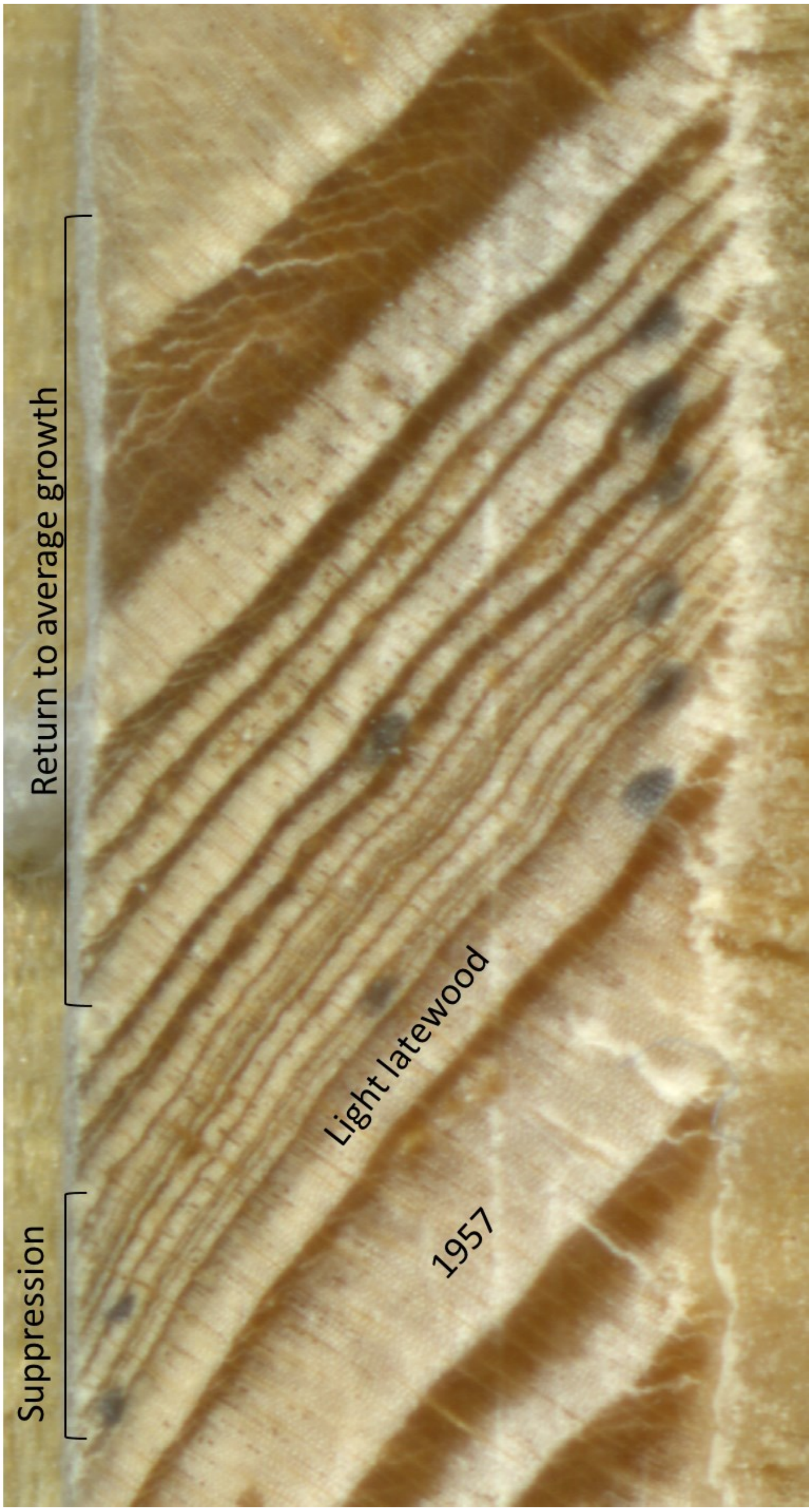

Figure 11. Suppression identified in Rose Lake cores showing indicators of larch sawfly outbreak between 1958 and 1970

However, the rings in this period resemble standard rings and lack the thin or under developed latewood, characteristic of rings during the 1986 and 1987 outbreaks. During the sampling excursion, beetle galleries were also observed on many of the standing dead tamarack but were not described in detail.

Quantifying the suppressions as outbreaks in the program OUTBREAK was an iterative process. I used OUTBREAK to quantify outbreak events using modified tussock moth parameters. The parameters were refined for identifying larch casebearer outbreaks to include a suppression of more than -1.50 standard deviations from normal growth, a suppression lasting three to four years, and a rate of increase in growth of 1.000.

Two suppressions were identified in the Rose Lake samples dating from 1942 to 1947 and 1958 to 1970. The 1958 to 1970 outbreak is only covered by the earliest portion of the non-host chronology (Figure 10). The most recent of the suppressions was covered by the non-host species, but there were too few samples from the non-host to get an accurate quantification using OUTBREAK. The 1958-1968 outbreak does show many of the indicators of a larch sawfly outbreak including a severe decrease in growth for ten years, a light latewood in the first year of the suppression, and a gradual return to pre-outbreak growth in one sample. There are documented outbreaks in Canada for this time period in eastern Quebec and northern Manitoba. This pattern is also present in four other samples but they are missing the light latewood and the suppressions are less severe.

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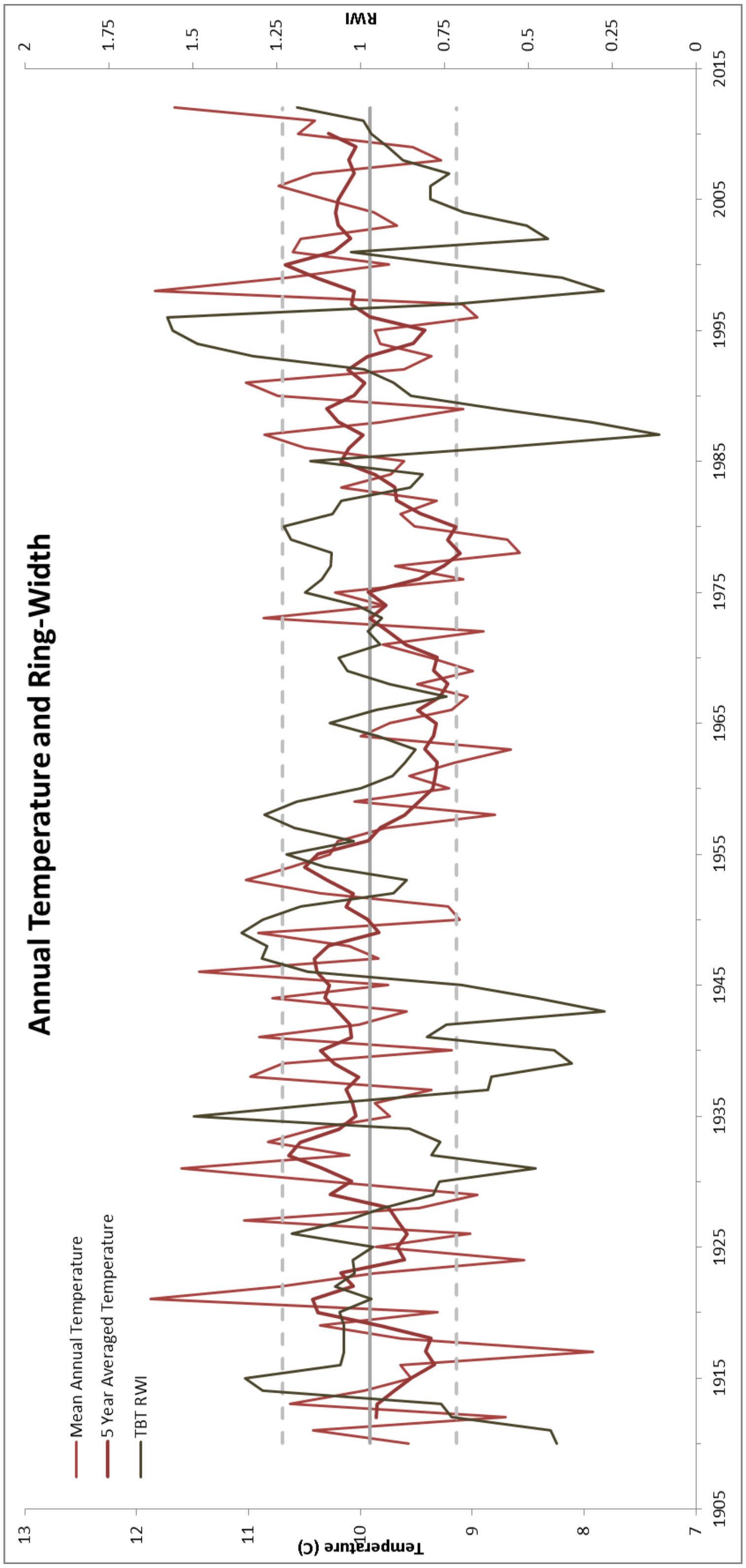

Figure 12. Plot of annual temperature (thin red line), five year averaged temperature (thick red line), and ring-width indices (brown line).

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Climate Comparison

Climate response showed slightly complicated results. Over the entire record, tamarack had a fairly weak response to climate. However, when looking at 25 year moving windows, patterns of response begin to emerge. Aside from the maple residual, birch, and Rose Lake total ring-width residual chronologies, significant climate responses were limited to temperature. The tamarack at Tamarack Bog had a correlation between -0.208 and -0.219 to September temperature of the previous year for all residual chronologies. Tamarack latewood and total ring-width in this location also had a significantly positive relationship to temperature in June of the previous season (r = 0.219). The significant climate correlations for birch at Tamarack Bog were negative responses to previous July PDSI in the standard and residual chronologies (r = -0.247 and r = -0.240 respectively).

Tamarack at the Rose Lake site had a few significant responses to climate. There were no statistically significant correlations in the earlywood standard and residual chronologies. The latewood standard chronology had a -0.210 correlation to previous November temperature, 0.154 correlation to previous June PDSI, and -0.093 correlation to previous October PDSI. The residual latewood chronology had a -0.224 correlation to current February temperature and a 0.232 correlation to March temperature. The total width residual chronology had significant responses to previous August and December precipitation and previous October and November PDSI with correlations of -0.194, 0.186, -0.079, -0.075 respectively. The total width standard chronology had a significantly negative correlation to previous October PDSI (r = -0.088). Maple at the Rose Lake site had a significantly negative response to current July, August temperature, and previous June PDSI (r = -0.264, -0.259, -0.160 respectively) and a significantly positive response to previous November temperature (r = 0.309) (Figure 13 and 14).

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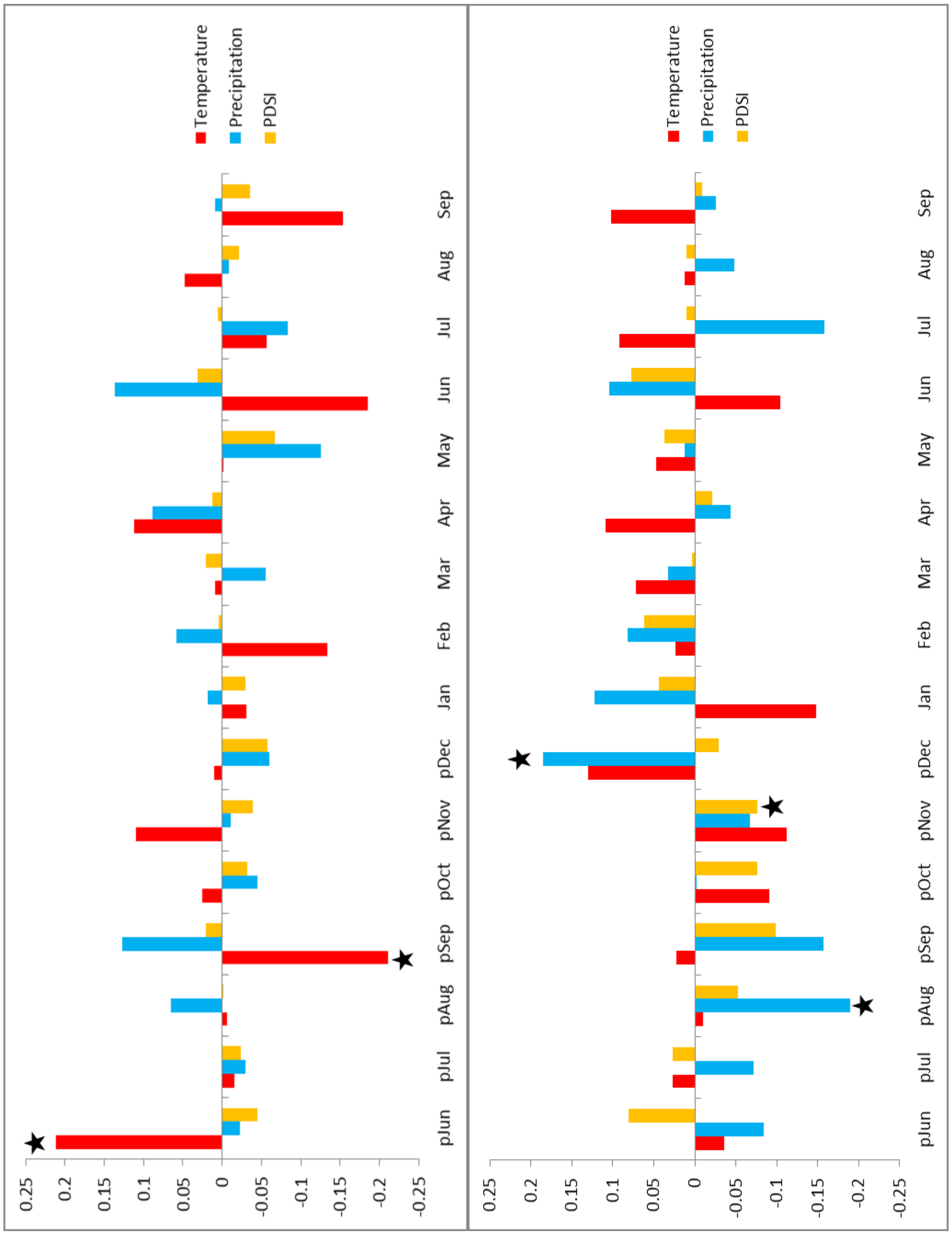

Figure 13 and 14. Bar graphs showing correlations of Rose Lake (right) and Tamarack Bog (left) total residual width and climate variables. Significant values are indicated with a black star.

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The outcomes of the moving climate response analysis were very similar between all of the chronologies at each site so general results from the sites will be presented. All years given are the end of the 25 year window of analysis (1930 = 1905-1930). From 1930-1960 tamarack at the Tamarack Bog site in Indiana had strong negative responses to May, June, and July precipitation and June temperature (Figure 15a). Between 1962 and 1985, a decrease or reversal in the sign of the correlation values is observed. With this change, there is an additional positive response to May and August temperature, and June precipitation (Figure 15a). After 1985, the climate correlations begin to return to the pattern seen at the beginning of the series with the addition of new strongly negative responses to May, June, and July temperature in 1983, 1988, and 1997 respectively. There are also strong positive responses to June precipitation between 1962 and 2000, and strong negative responses to July precipitation between 1990 and 1997.

At the Rose Lake site, moving climate response analysis showed strong positive responses to July temperature from 1955 to 1983 and September temperature from 1986 to 2002 (Figure 14b). Strong negative responses to May precipitation and June temperature were observed from 1954 to 1983 and from 1985 to 2009 respectively.

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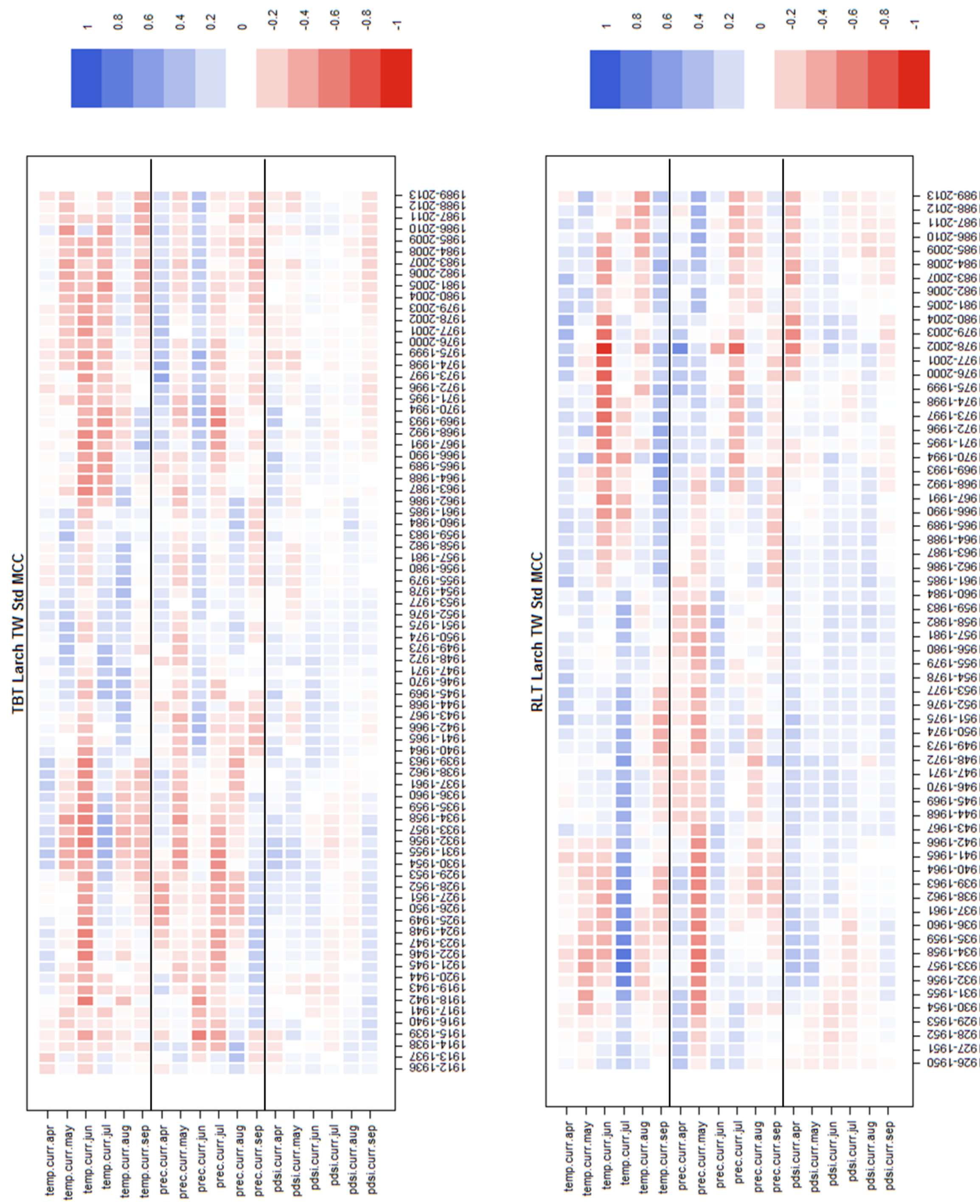

Figure 15 a/b. Moving climate response analysis plots for temperature, precipitation, and PDSI showing correlation values (red and blue) for a given window in the analysis. Higher correlations are depicted in a darker shade of blue and lower in a darker shade of red. The maximum response was a 0.580 correlation with TBT Larch Total Width and 1933-1957 temperature.

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Chapter 5

DISCUSSION

Chronologies and Outbreak Events

Due to their strong interseries correlation and high mean sensitivity values, samples analyzed in this study are good candidates for reconstructions in this geographic area. However, the short series length is challenging when attempting to do long term insect outbreak studies (Jardon *et al.* 1994, Girardin *et al.* 2002, Girardin *et al.* 2005). The detrending process was successful in these short series at removing the growth trend without removing much of the short term variation. Series detrending models were carefully selected to avoid any introduction of artificial increases or decreases in growth. The increases in growth in the outer two years of the chronology were consistently observed in the raw ring-widths and were therefore preserved through the standardization process.

The presence of suppressions and anomalous ring characteristics during outbreak events suggests tamarack are good recorders of larch casebearer outbreaks. Missing rings in these periods show that intense defoliation can cause dramatic reductions in growth. When compared to growth rate reductions in studies from southern Ontario and Idaho (Benoit and Blais 1988, Alfaro *et al.* 1991), impacts to radial growth are far more severe. Though the intensity of the initial outbreak event is similar to that of the larch sawfly, the larch casebearer outbreaks are shorter in duration, lasting between three and four years. Larch sawfly outbreaks are consistently

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between four and fifteen years and have a slower return to average growth. Also, visually inspecting the ring width patterns helps to control for effects of tree structure changes. For instance, identifying ring characteristics such as traumatic resin ducts and poorly developed latewood help to control for changes in tree structure.

Some trees did have a sustained decrease in growth and ring characteristics of branch damage after the first outbreak period in 1986 lasting around 25 years. As many of the trees experienced mortality of branches, this suppression was likely caused by a reduced photosynthetic ability of the tree. Similar suppressions in growth were also observed by Alfaro *et al.* in their 1991 study on western larch. They found that growth after an outbreak event was consistently less than expected based on non-host chronology (Alfaro *et al.* 1991). This would likely make them increasingly susceptible to further outbreaks. An example of this can be seen in Figure 10. The period of suppressed growth in the tree highlighted by the letter “B” shows the period of the first larch casebearer outbreak. The initial outbreak pattern can be seen in 1986 with the suppression followed by 4-5 years of below average growth. After 1990 the tree experiences another traumatic event which causes the tree to lose vitality in its branches. The tree produces traumatic resin ducts in the beginning of 1991 and the rings that follow have a poorly lignified boundary. This morphology closely resembles rings in trees affected by mortality of branches (Schweingruber *et al.* 2006, pg. 156). The tree previously described eventually succumbed to the 1997 outbreak event. This is likely a result of their inability to produce sufficient reserves with substantially damaged canopies. Considering the number of dead trees with substantial loss of branches and cores with highly suppressed outer rings, it is likely that many of the other dead trees in this stand were affected in a similar fashion.

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A visual comparison between temperature records and outbreak events show temperature is a potential factor in outbreak initiation. In the first year of each outbreak event (1986 and 1997), there are temperatures above one standard deviation from the mean. There are other periods where mean annual temperature is one standard deviation higher than the mean, but there were no outbreaks seen in these periods. Temperature may be a factor in the initiation of an outbreak event, but these other years of high annual temperature indicate there are additional factors on larch casebearer outbreaks. Evidence supports temperature can limit insect populations (Ungerer *et al.* 1999, Marini *et al.* 2012) so it will be important for future research to develop larger datasets of insect outbreaks to further explore additional driving factors of larch casebearer in this region.

The 1958-1968 suppression observed in cores at Rose Lake show some evidence of insect outbreak. The five oldest samples show suppressions similar to those seen in the most recent larch casebearer outbreaks. Climate responses are also very similar to those of the recent record. It is possible that this suppressed period was caused by an outbreak of the larch casebearer but the suppression morphology seen in RLT014 (Figure 11) suggests larch sawfly could be an additional factor. Additional sampling to achieve a higher number of samples of both host and non-host for this timeframe would shed better light on the cause of this suppression.

There is evidence indicating eastern larch beetle is present in both of these stands. This species is a native insect across North America, and tends to cause secondary infestations. The presence of beetle galleries in both sites on dead or downed tamarack indicates there is an additional factor present in these stands. Until the mid-20th century, beetles have been relatively innocuous, causing very little mortality in stands. Continued observations of the eastern larch

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beetle in this area is important to determine the additional impact they have on the already stressed trees in Tamarack Bog, and the young tamarack in Rose Lake.

Climate Response

Tamarack are primarily found in swamps or bogs where water is very close to the surface. Each of these study sites are located in drained lowlands controlled by a dam at Tamarack Bog, and an outflowing stream network at Rose Lake. A lack of a response to precipitation is what one would expect given these conditions. If the majority of the water needs are met by the marshy environment, growth should be limited by another variable. One interesting response seen in the later portion of the moving climate response analysis at the tamarack bog site is the increase in the negative correlation to growing season temperature. The trees begin responding with increased stress as temperatures warm in the last few decades. A similar response to growing season temperature appears at the beginning of the tree-ring record which dissipates as temperatures cool in the mid part of the 18th century. Comparing these periods with spatial weather patterns for these warm and cool years shows that temperature isn't the primary limiting factor in this part of the species range. However, the increase in stress to temperature indicates that there is some connection to temperature.

It is also important to consider insect outbreaks when examining climate analyses. These changes in the climate response could be influenced by the effects of insect outbreaks during these periods. This response analysis could potentially be picking up on the insect outbreak signal in the tree-rings and is conveying those values instead. This illustrates the importance to check for insect outbreaks when performing climate reconstructions. With long term tree-ring records, it is often impossible to find records of insect outbreaks beyond the modern record. But

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by exploring for and removing insect derived suppressions, there should be reductions in error seen in the climate reconstruction.

Climate response analysis for red maple at the Rose Lake suggests temperature is significantly affecting these trees. This supports the general ecological model which states that populations located at northern extents are limited by temperature. The northern geographic range boundary for red maple runs just across the northern side of the Great Lakes (Figure 16). Rose Lake is not located in a tundra, but it may be close enough to this border where temperature starts to play a role in ring development. An inverse response to February temperature in the latewood residual chronology warm Februaries likely initiation growth and any subsequent frost or cool events, which would damage the newly forming buds. The maple chronology from Rose Lake had a somewhat more simple story. The positive response to previous September and November temperature suggests maple are better able to produce increased stores for the following growth season if fall temperature stay warm. Likewise, if temperatures were to drop in an early onset of winter, growth and the storing of nutrients would be halted by the drop in tree productivity.

Stand Replacement and Regeneration

Sample age and recruitment times suggest regeneration at Tamarack Bog has been affected by a change in disturbances in recent decades. Tamarack traditionally do very well with disturbances like fire and clearance. It is very shade intolerant and requires open spaces to grow. The recruitment event between 1910 and 1924 is likely the result of a stand-level disturbance-created openings for a large amount of seedlings to establish. Throughout the range of tamarack, fire and wind are the mechanisms for canopy openings (Johnston 1990). Considering the historical presence of humans at this site, it is also possible the area was logged for fence posts

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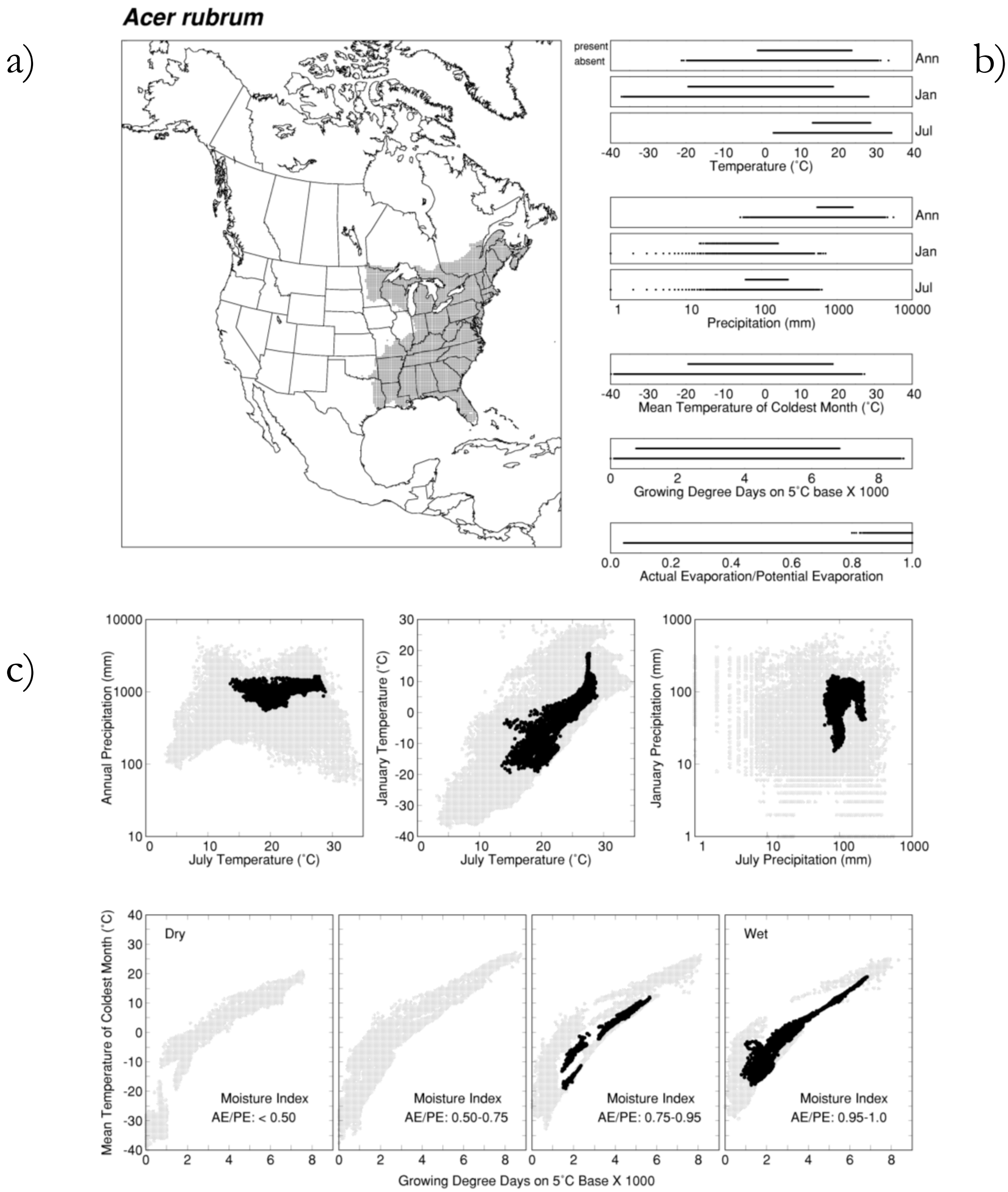

Figure 16. a) A range map showing the distribution of points where red maple are present, b) Plots showing the climate where red maple are present (top line) and absent (bottom line), and c) bivariate plots illustrating potential interactions between tree and climate with points where red maple are present in black and absent in grey (Thompson *et al.* 1999).

which was tamarack's primary use at the turn of the 20th century. This event would have opened a space in which seedlings could germinate. This recruitment is followed by a 30-year break in establishment. There was a strong negative correlation to temperature during this period of no establishment. This period has six of the fifteen years with above average temperatures: 1931, 1933, 1938, 1939, 1941, and 1944. There is also the possibility this suppression is caused by an early outbreak of larch casebearer as they moved through the Great Lake's region. The ring characteristic indicators for outbreaks are largely missing from this period, but there is an inverse relationship to temperature during this period, similar to that seen in the recent outbreaks of larch casebearer.

The period between 1950 and 1980 consistently has some of the largest and most complacent rings in the whole chronology. This is the most consistent cool and moist period in the record as well. Temperatures drop below average and precipitation tends to stay the same. There is a positive correlation to both growing season temperature and precipitation during this time frame. This is a climate pattern more typical of a site farther north which is likely more conducive to tamarack regeneration. Once temperature begins to rise again in the 1980's, growth response becomes negatively correlated to temperature and new saplings start to disappear. These variations in temperature can be seen spatial as well. Figure 17 shows the spatial distribution of climate which is favorable to tamarack growth, determined by where tamarack are currently found. The isolines depicted in the map indicate a line of 24°C which has been determined to be upper end of tamarack's climate range. The isolines for the cool 1976, warm 1931 seasons, and the last 30 year average temperatures show that tamarack is consistently within favorable climate and could potentially move farther south. This demonstrates that temperature isn't the primary factor in limiting tamarack's geographic distribution and it is likely

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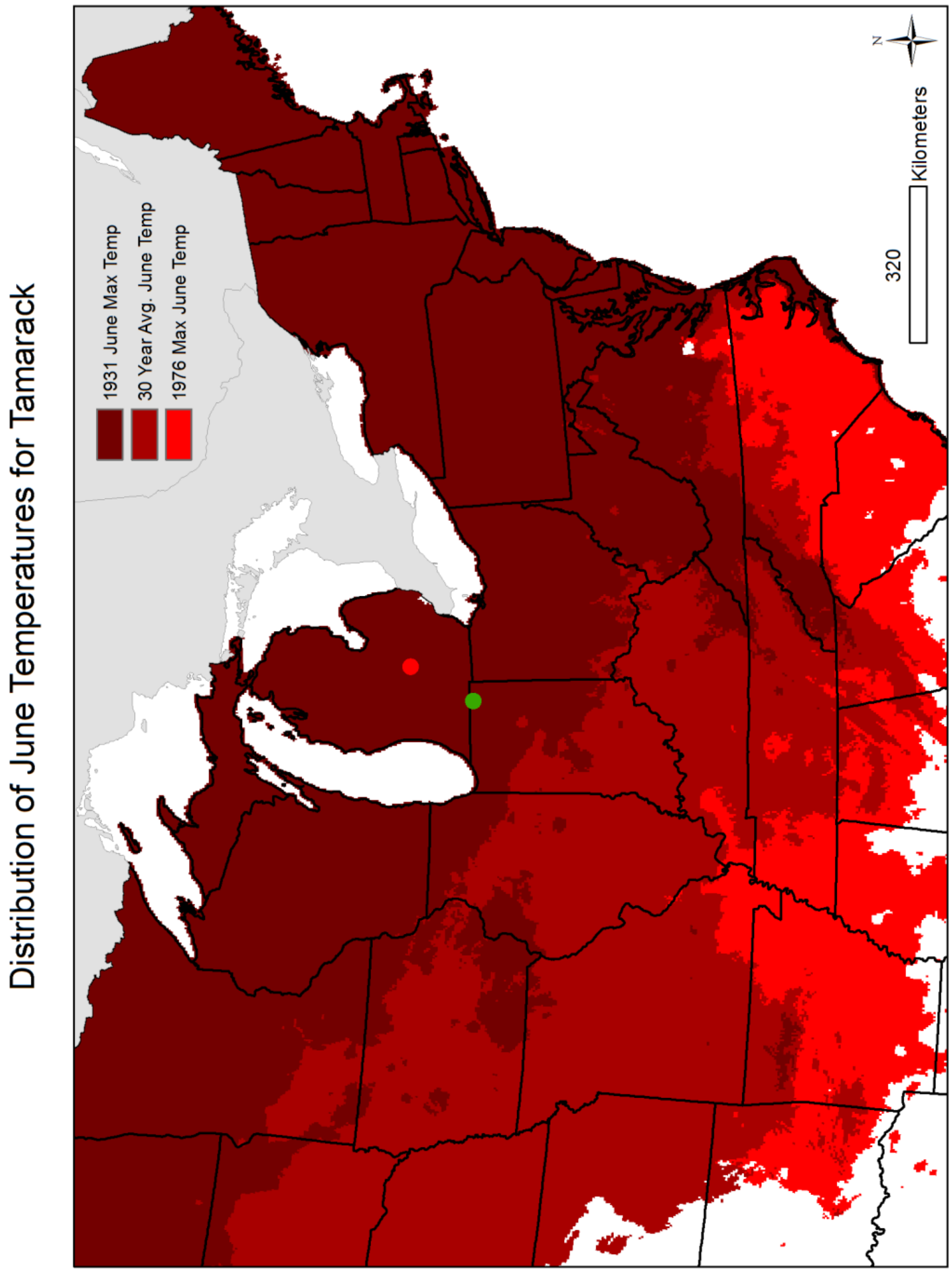

Figure 17. A map showing the warm, cool, and average temperatures for June across the United States. This map shows that climate does not play a role in limiting tamarack geographic distribution because tamarack would be present throughout much of the average and above average areas if it were limited by temperature.

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some other factor. Because tamarack are poor competitors in shade conditions, it is likely that species competition has a larger role in the southern limit.

The current structure at the location suggests temperature and increased stress from defoliating insects is limiting the regeneration of tamarack at this site. The youngest tree sampled in Tamarack Bog is more than 30 years old. This has important ramifications for the composition of forests to come at this site. As global temperatures rise, there will likely be increased stress on the trees at this site and they will likely become more sensitive to defoliation by phytophagous insects. As more mature trees succumb to the effects of insect outbreaks, no tamarack will be regenerating to replace them as they die. The forest composition will ultimately shift from a tamarack dominated woodland, to a broadleaf dominated woodland. The last vestigial populations of tamarack would be extirpated from this site and biodiversity would suffer. It will be important to examine what species are regenerating under these tamarack to see what will replace tamarack on this landscape.

The stand at Rose Lake seems to be doing much better. Overall the trees are much younger. The majority of the trees date to around 1970 with the exception of a few which date back to 1924. The area had been logged fairly extensively in 1910 (Ackney 1988) so these trees could be offspring from that clearing. The recruitment of maple at this location follows very closely that of the tamarack. With the exception of the oldest tamarack, both species started growing about the same time and with similar recruitment rates. Currently there are no observed tamarack seedlings, but the youngest tamarack in the stand is about 14 years old. The presence of these young tamarack indicate tamarack has been able to reproduce, however, with decreasing success. This is likely due to the very dense nature of the current site. Currently, the Rose Lake site is dominated by tamarack and red maple trees and dense deciduous undergrowth. This dense

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understory is limiting the amount of sunlight reaching the ground and if tamarack seedlings are unable to get enough light in the first five years of growth, they are not going to survive. The pattern seen at Rose Lake is one of competition. Tamarack are slowly being outcompeted by deciduous, more shade tolerant species. Eventually the tamarack will reach maturity and the shade tolerant species will take over.

It could be quite beneficial to reintroduce fire into the systems. However, caution is advised for Tamarack Bog site due to the potential loss of seed bank from the denuded trees. If these stressed trees were unable to produce proper cones or fully developed seeds, the seed bank could be drastically lower than a healthy forest system. It would be prudent to first determine the reproductive status of the stand before clearing it. Various techniques of burn, slash and burn, or logging of non-tamarack trees and subsequent seedling counts should be studied before further action is taken. Such precautions would be excessive at Rose Lake because the trees are not as stressed as their southern counterparts. Considering the density of understory shrubs at Rose Lake, repeated low intensity prescribed burns would likely be most effective at suppressing the broadleaf species. If thinning of trees occurs in either site, it will be important to remove any dead wood which can accumulate populations of eastern larch beetle which can transfer to living tamarack.

Chapter 6

CONCLUSION

I have determined that it is possible to distinguish suppressions caused by outbreaks larch casebearer from those caused by larch sawfly. The ring width patters caused by larch casebearer in this study were noticeably different from the characteristics caused by larch sawfly identified in established sawfly literature. The larch casebearer identification parameters should be replicated in future studies to examine spatial variation or unity of the tree-ring signature.

Tamarack in Indiana also exhibit signs of sensitivity to increased annual temperatures. Historic and current growth responses indicate tamarack are more stressed when the average annual temperate is higher than average. However the geographic distribution of favorable temperatures farther south than Indiana indicates that temperature is not a primary limit to tamaracks southern distribution. Increased annual temperatures do appears to be a factor in triggering larch casebearer outbreaks. These outbreaks are exerting additional pressure on climactically stressed tamarack, reducing the ability of the trees to survive and reproduce in this region. Future research will need to examine more insect outbreak periods to determine a more complete list of predictors.

The combination of stress from increased temperature, repeated outbreaks of larch casebearer, predation from the eastern larch beetle, and the lack of regeneration at the site indicates tamarack are in danger of being extirpated from Pigeon River State Fish and Wildlife

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Area if the status quo is maintained. Repeated defoliation events are likely making the trees more susceptible to eastern larch beetle, which is known to cause mortality in tamarack. If eastern larch beetle responds like other bark beetle species, an increase in temperature in the area is likely to make their impact on the stressed tamarack population increasingly severe. A similar result can be expected for Rose Lake Wildlife research area though with a different driving factor. It will be important for local managers to adapt their management styles to include fire or clearing of broadleaf plants to restore the natural establishment regime. Tamarack provide a unique habitat for birds and other wildlife. It is important to remember that as climate changes, ecosystems like this one will continue to change. Weighing the preserving a species or allowing them to move out of the region naturally as climate shifts will be the philosophical debate of the current generation of scientists. Future research should focus on developing a network of climate response studies along the southern margin of tamarack to see if increasing stress to temperature is holds true across the greater geographic range of tamarack.

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